The Larval Nutrition of *Minettia flaveola* and *Phaonia parviceps* and its Significance to the Hawaiian Leaf-breeding *Drosophila*

(Diptera: Lauxaniidae, Muscidae, Drosophilidae)

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The purpose of the present report is to point out the similarities and differences in the larval ecology and nutrition of several species in the two Dipteran families, Lauxaniidae and Drosophilidae. The habit of mining in decaying detached leaves by representatives of these two families presents an unusual opportunity to study the dynamics of host plant selection and related phenomena such as competition and nutrition. The leaf-breeding habit in the Drosophilidae is known only in the Hawaiian Islands and is universal in the genus *Antopocerus* and three related groups of species within the genus *Drosophila* (Heed 1968). Species in other groups and in the genus *Scaptomyza* also breed in fermenting leaves and the habit appears to have evolved independently several times. In total there are approximately 80 to 100 leaf-breeding species endemic to the Islands. Holarctic members of the Lauxaniidae have long been known to occupy this niche (Hering, 1951; Oldroyd, 1964). However until the present report no one has compared larval nutrition in the drosophilids and the lauxaniids. The overall similarity of the rotting leaf niche available for the two groups is so striking that a detailed account of recent observations and tests is given below.

The breeding biology of the Hawaiian leaf-breeders has been compared previously (Heed 1971) to the unusual biology of *Rhagoletis* (Tephritidae), as observed by Bush (1969).

RESULTS AND DISCUSSION

On October 10, 1972, eggs and first-instar Dipterous larvae were discovered in a redwood forest by one of us (WBH) at Prairie Creek Campground, north of Orick, Humboldt County, California, on the surface of fermenting leaves littering the ground beneath a California Bay tree (*Umbellularia californica* (H. & A.) Nutt.). The majority of eggs and larvae were acalyptrate but 1 predatory larva and an egg of a species of Muscidae were also noted. The leaves were stored on moist sand in

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jars at 68° F at U. C. Davis, and adults were first noticed on 24 January, 1973. They were identified as *Minettia flaveola* (Coquillet) (Lauxaniidae). Many puparia and puparial cases were found within the leaves, but only 3 puparia were washed from the sand. On 28 December, 1972, another collection was made at the same tree and large third-instar larvae were observed mining within the leaves. On 21 June, 1973, no larvae were found and the leaves were mostly dry.

Three other collection localities produced fermenting Bay leaves that contained larvae: (1) along the Carmel River at Carmel Valley, Monterey County, 25 November, 1972; (2) McDonald Ranch at Pope Valley, Napa County, 22 January and 5 February, 1973; and (3) 5 miles west of Lake Berryessa on State Route 128, Napa County, 1 February, 1973. In addition to *M. flaveola*, the Napa County samples produced another lauxaniid which proved to be a new species of *Homoneura*. Predaceous larvae were observed in all of the collecting sites, and one was seen to attack and consume a lauxaniid larva in the latter McDonald Ranch sample. The adult of this larva was reared and identified as *Phaonia parviceps* Malloch (Muscidae). The larva of *P. keilini*, has been reported to prey on mosquito larvae (Oldroyd 1964).

The Prairie Creek collection in October was assayed for yeasts. Samples were taken from the surface of 3 leaves (2 of which had tiny larvae on the surface) and innoculated on acid-malt-agar plates in the field by direct plating and by previous dilution in 2 ml. sterile water (Table 1). Five of the species were represented by less than 10 colonies each in all the plates. *Rhodotorula minuta* var. *minuta* was abundant (1000 colonies) on 1 leaf and *Torulopsis fujisanensis* was common on 2 leaves (100 colonies each). Most of the species are considered to be widespread and all are nonfermentative. *T. fujisanensis*, however, has not been reported from the Pacific Northwest (Phaff et al. 1972). In addition to the yeasts, bacteria and mold colonies were abundant on the original plates.

The collection from Carmel Valley was assayed for yeasts from the somewhat fluid interior of the fermenting leaves. Five leaves, 4 with a large larva in each, were sampled by direct plating and by the addition of sterile water in the leaf. All slants were made on acid-malt-agar plates. Only 28 yeast colonies appeared among many mold colonies in 9 plates. Twenty-four of the colonies originated from the leaf with no larvae (Table 1). Two leaves produced 2 colonies each and the two remaining leaves produced no yeast at all.

The significance of these observations and tests lies in the similarities

TABLE 1. Yeasts isolated from fermenting leaves of the California Bay Tree.

Species	Total no. colonies	California localities	Yeast niche
Cryptococcus albidus (Saito) Skinner var. *diffluens* (Zach) Phaff et Fell	4	Prairie Creek (3 leaves)	Surface
Cryptococcus laurentii var. *laurentii* (Kufferath) Skinner	1	"	"
Leucosporidium scottii Fell, Statzell, Hunter et Phaff	5	"	"
Rhodotorula minuta var. *minuta* (Saito) Harrison	1000[1]	"	"
Torulopsis fujisanensis Soneda	230[2]	"	"
Candida moscorum di Menna	9	"	"
Candida buffoni (Ramirez) Van Uden et Buckley	2	"	"
Pink colonies (lost)	43[3]	"	"
Cryptococcus albidus var. *diffluens*	1	Carmel Valley (5 leaves)	Interior
Cryptococcus infirms-miniatus (Okumuki) Phaff et Fell	26[4]	"	"
Debaryomyces hansenii (Zopf) Lodder et Kreger-van Rij	1	"	"

[1] 1 leaf.
[2] 2 leaves.
[3] Probable identification: *Cryptococcus infirms-miniatus*.
[4] 24 colonies from one leaf, no larvae; 2 colonies from feces of single larva in a second leaf.

and differences they exhibit with the identical larval leaf niche in the Hawaiian Archipelago which is occupied by a large number of endemic species in the genus *Drosophila* (Drosophilidae) (Heed, 1968; Kircher, 1969; Kircher and Heed, 1970; Carson et al., 1970). There are 4 major similarities between the 2 regions. (1) Both the coastal region in northern California and the windward slopes in the Hawaiian Islands are belts of equable temperatures and high humidity for a major portion of the year. This is important for the constancy of the resource (evergreen foliage) and the slow soft-rot decay of leaves by mold and bacteria. (2) The fresh leaf of the Bay tree has a familiar aromatic fragrance when crushed. When the leaf is fermenting on the ground its scent is prevalent in a somewhat modified form. All of the leaves utilized by *Drosophila* larvae in Hawaii such as *Cheirodendron*, *Tetraplasandra*,

Ilex, *Clermontia*, *Pelea*, *Myoporum*, *Myrsine* and others have their own characteristic aroma produced by the breakdown products and their essential oils. These distinctive scents are believed to play a major role in the very high host plant specificity observed in the Hawaiian leaf breeders and probably are also important to the lauxaniids discussed here. Mr. Ray Miller (personal communication) relates that 7 species in 5 genera of the Lauxaniidae have been reported in rotting leaves. Dr. B. A. Foote, Kent State Univ., and R. Miller have reared species of the genera *Homoneura*, *Lyciella* and *Minettia* from decaying leaves of sugar maple, sassafras, alder, elm, and wild black cherry in deciduous forests in Ohio (personal communication). (3) The nutrition of the Hawaiian leaf-breeding larvae is known to be based chiefly on bacteria and broken down plant parts for the reason that no yeast of any consequence has been isolated from the interior of the leaves (Robertson et al. 1968). Also the leaf-breeding species are notoriously difficult to raise on laboratory media containing yeasts. However, a variety of yeasts have been isolated from the rotting leaf exterior in Hawaii (H. J. Phaff and M. W. Miller, personal communication). The observations in the present report are similar to the extent that the interior of the rotting leaves significantly lack the variety and density of the yeasts found on the leaf surfaces. Hering (1951) considers that the lauxaniids which are found in rotting leaves are modified leaf miners that had a saprophagous origin. (4) Both fly-substrate systems in California and Hawaii support larval predators in the family Muscidae. In Hawaii the genus is *Lispocephala* (Heed 1968).

One of the major differences between the lauxaniids and the drosophilids is that the former oviposit on the leaf surface and the first-instar larva presumably develops there for a while before entering the leaf. Up to this time, the major nutritional source could come from yeasts. The Hawaiian *Drosophila* insert the eggs into the mesophyll of the leaf with only the filaments emerging (Kambysellis and Heed 1971). Another difference is that pupation takes place within the leaf for *Minettia* and *Homoneura* but in *Drosophila* it occurs several inches below the soil surface. Finally, *Drosophila* apparently do not use the leaf niche in North America (Carson 1971). Presumably the absence of native lauxaniids in Hawaii (Hardy personal communication) may have been a contributing factor for the occupation of this niche by *Drosophila*.

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